A CARBONIFEROUS *SELAGINELLITES* WITH *DENSOSPORITES* MICROSPORES

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ABSTRACT. *Selaginellites canonbiensis* sp. nov., a small lycopod cone compression from the Upper Carboniferous of Scotland, is described and figured. Its megaspores agree with the spore species *Setosisporites hirsutus*, and its microspores are of the *Densosporites* type. Populations of spores of these two types associated in the Shafton Coal, Yorkshire, compare closely with those from the cone. This correlation suggests that *Selaginellites* may have been the dominant component of the vegetation which gave rise to *Densosporites*-rich coals of the durain type

INTRODUCTION

IN the last thirty years maceration studies of Palaeozoic rocks, particularly coals, have resulted in the description of several hundred species of isolated spores and pollen. Inevitably, the parent plants (and so the true affinity) of many of these types is unknown. For stratigraphical work this aspect is usually regarded as of secondary importance, and interest has centred on the vertical and horizontal distribution of the various spore types. However, these records of isolated spores have acted as an incentive to closer study of the spores contained in fossil fructifications. As this information accumulates it becomes possible to interpret a Palaeozoic spore assembly in terms of its parent plants, as in the pollen analysis of Quaternary peats.

One of the commonest of Carboniferous 'small spores' of which the parent plant has hitherto been unknown is *Densosporites*. This paper describes an Upper Carboniferous herbaceous lycopod cone which contains spores of this type; its megaspores also prove to be of a type long known isolated from Upper Carboniferous coal macerations. This correlation of *Densosporites* with a herbaceous lycopod has significant ecological implications which are discussed below.

It is a pleasure to be able to express my thanks to Dr. F. W. Anderson, Chief Palaeontologist of the Geological Survey, who has made possible the loan and examination of the holotype from the Kidston Collection. I am also grateful to Professor J. Walton for permission to examine a slide in the Kidston Slide Collection in the University of Glasgow, and to Professor T. M. Harris F.R.S. for helpful advice.

DESCRIPTION OF THE CONE

The lycopod cone described below as *Selaginellites canonbiensis* sp. nov. (Pl. 44, figs. 1–3) is a compression in dark shale from the Byre Burn Group of the Canonbie Coalfield, Dumfriesshire, Scotland. As the exact relationship of this group with the Coal Measures of other areas has not been established, the age of the cone can only be given as Westphalian (Upper Carboniferous). Associated with it on the same piece of shale are *Sphenophyllum cuneifolium* (Sternb.), *Asterophyllites equisetiformis* (Schloth.), *A. sp.* cf. *charaeformis* (Sternb.), and several leafy shoots of the *Lycopodites* type.

The cone compression shows a series of sporangia arranged spirally around an axis which they completely conceal. Projecting beyond each sporangium and appearing to

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come from beneath it is the free end of the sporophyll lamina. This is most easily seen at the side of the cone (Pl. 44, fig. 2), where the lamina can be seen turned parallel to the cone axis. In the living cone these overlapping scale-like distal ends of the sporophylls would have covered and protected the sporangia, as in a typical *Selaginella* cone. The sporangia, as seen in the compression, consist largely of the 'mummified' remains of the spores they contained. The lower sporangia can be seen under a binocular microscope to contain megaspores, as their outlines show clearly through the coalified remains of the sporangial wall. This megaspore-bearing zone is succeeded by one of apparently smooth, uniform sporangia in the apical part of the cone. A fragment removed from this zone and macerated for about twelve hours with Schulze's solution (concentrated nitric acid and potassium chlorate), followed by ammonia solution, yielded hundreds of microspores (Pl. 44, figs. 4–7). These were mounted in glycerine jelly. A number of megaspores were removed from the cone with a needle and treated with Schulze's solution followed by ammonia, to remove adhering coaly matter. Some of these were mounted in air cells as opaque objects for examination by reflected light; the remainder were further treated with Schulze's solution until transparent, washed, and mounted in balsam for examination by transmitted light (Pl. 44, figs. 9 and 10). When using Schulze's solution for clearing spores in this way (as distinct from freeing them of coaly matter) treatment with ammonia was omitted as this not only darkens them but also may corrode the spore wall.

The cone is apparently intact at the apex, but the base is incomplete. The difference in the appearance of the microsporangia and megasporangia makes the transition between the two zones (about half-way up Pl. 44, fig. 2) quite evident. A single megasporangium occurs slightly above this level, but the transition is otherwise abrupt.

Apart from their gross morphology nothing in the way of structure of the sporophylls can be seen, and no cuticle was obtained from the sporophyll lamina.

THE MEGASPORES

The exact number of megaspores in each sporangium is not clear. The one megasporangium occurring among the microsporangia appears to contain only one tetrad; in the zone of megasporangia lower down the cone the outlines of the individual sporangia cannot be clearly discerned, but these, too, probably contained only a single

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EXPLANATION OF PLATE 44

Figs. 1–3 are photographed by reflected light; Figs. 4–11, by transmitted light.

Figs. 1–3. Holotype of *Selaginellites canonbiensis* sp. nov. 1, marked with white pointer, ×1. Photographed under xylol. 2, ×4. Note the *Lycopodites* type shoot to the left of the cone. 3, × 4, photographed dry, with oblique illumination from the bottom right.

Fig. 4. A group of microspores from *S. canonbiensis* sp. nov., ×130.

Figs. 5–7. Microspores from *S. canonbiensis* sp. nov., ×500.

Fig. 8. Microspore, *Densosporites sp.* cf. *loricatus* from the Shafton Coal, stained with safranin. ×500.

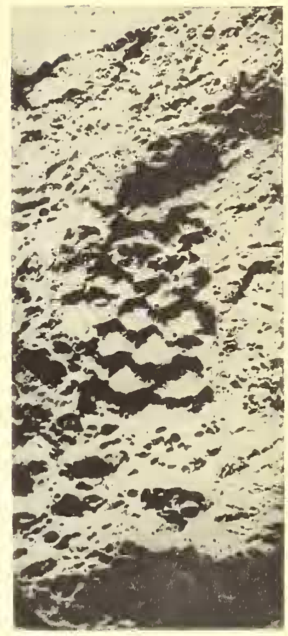
Figs. 9 and 10. Megaspores from *S. canonbiensis* sp. nov., ×50.

Fig. 11. Megaspore, *Setosisporites hirsutus* from the Shafton Coal, ×50. The spines appearing to be on the contact faces are in fact on the distal face of the spore, and are merely seen through the smooth contact faces.

Location of the specimens: Geological Survey and Museum, London. Figs. 1–3, Kidston Collection 3153. Figs. 4–6, Kid. Coll. 3153A. Fig. 7, Kid. Coll. 3153B. Fig. 8, Mik (C) 277. Fig. 9, Kid. Coll. 3154A. Fig. 10, Kid. Coll. 3154B. Fig. 11, Mik (C) 282.

1 x1

2 x4



3 x4

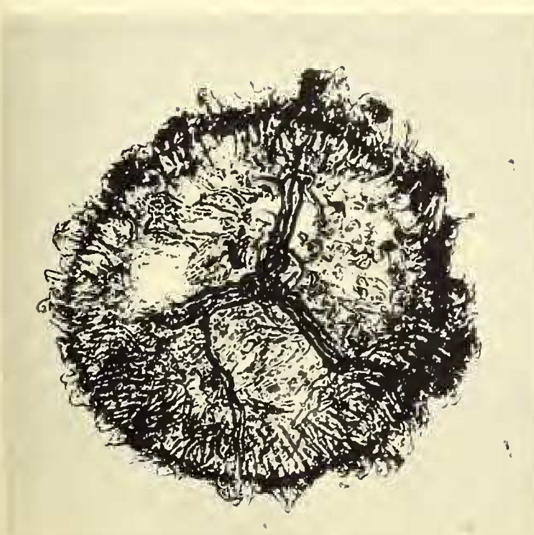
6 x500

5 x500

4 x130

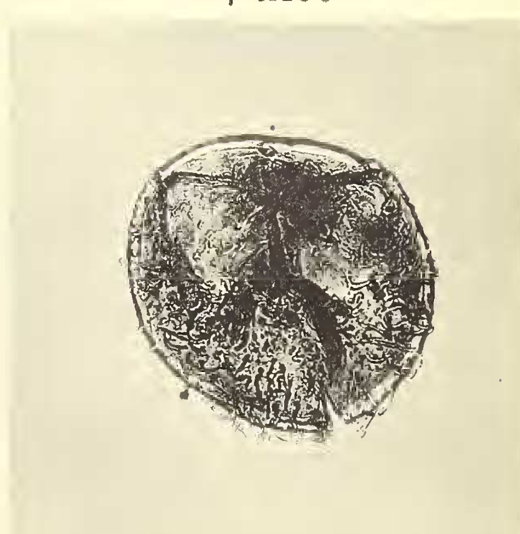
8 x500

7 x500



11 x50

10 x50



9 x50

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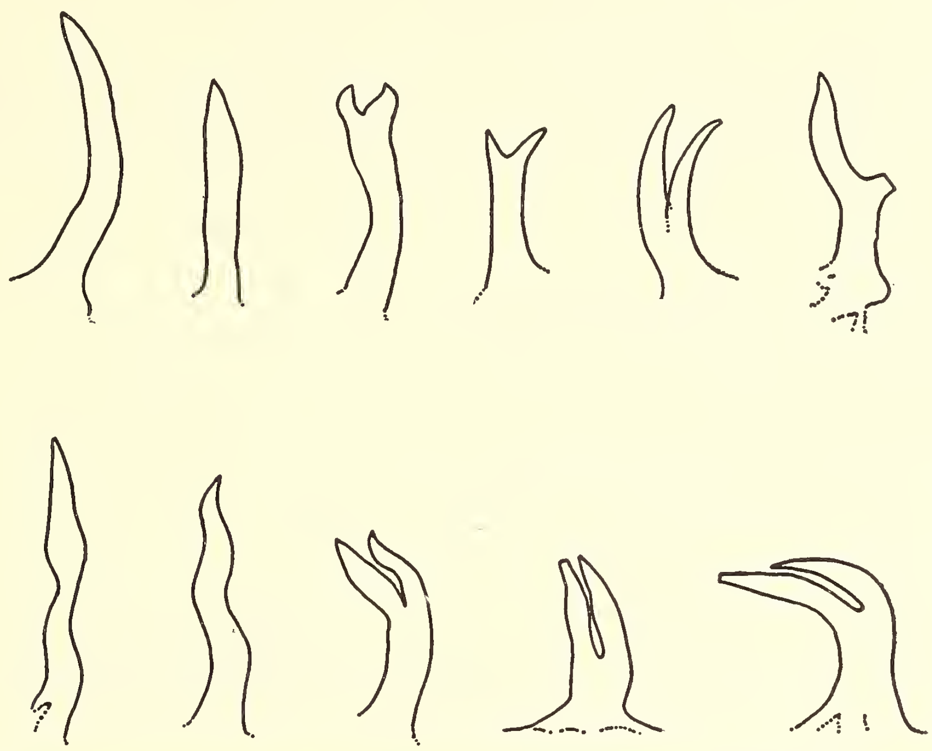
tetrad. From the size of the megaspores it is unlikely that there were more than four tetrads per sporangium at most.

The megaspores must originally have been more or less spherical, as the compressed spores have a circular outline regardless of their orientation when compressed (Pl. 44, figs. 9 and 10). They have a clear triradiate marking, and at the centre of the three ridges a small hollow globular prominence is present. The contact faces are smooth, but the remainder of the spore is uniformly covered with spines mostly around 60 μ long, which may branch once (text-fig. 1). The spines have a slightly expanded trumpet-



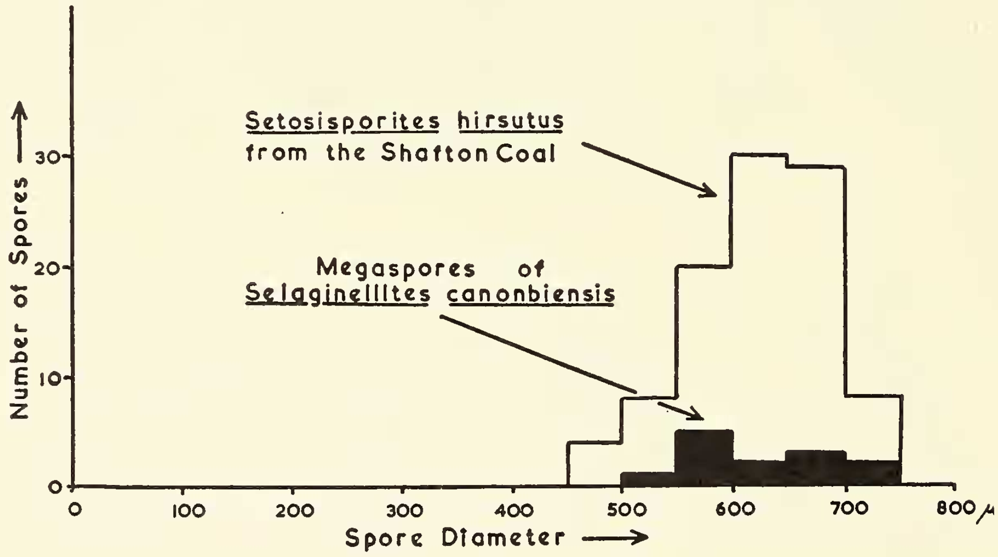
TEXT-FIG. 1. Spines from megaspores of *Selaginellites canonbiensis* sp. nov., $\times$400, showing variation in the branching. Each row of spines is from a single spore. (Slide 3154B, Kidston Collection, Geological Survey Museum: upper row, spore 5; lower row, spore 7.)

shaped base, but above this are more or less cylindrical for about two-thirds of their length, tapering in the apical one-third to a sharp point. They may branch at any level, but no more than a single bifurcation was seen. The branched and unbranched spines are mixed haphazardly, with the former in the minority. The triradiate ridges are about five-eighths of the spore radius as seen in specimens squashed in the equatorial plane. They have a fine suture running along their length, but no specimens were seen to have split open along this suture as though germinating. The contact faces are delimited mainly by their being rather thinner than the remainder of the spore wall, and by the abrupt cessation of the spines.

Megaspores similar to those occurring in *Selaginellites canonbiensis* sp. nov. occur commonly in Upper Carboniferous coals and are known as *Setosisporites hirsutus* (Loose) Ibrahim (or *Triletes hirsutus* of Schopf, Wilson, and Bentall 1944, Dijkstra 1946, and others). This type of megaspore is known from Upper Carboniferous coals from Germany, Holland, France, and Turkey (see Dijkstra 1946, Potonié and Kremp 1955 for full discussion of synonyms and range). The author has also obtained it from a number of British Upper Carboniferous coals. In a sample from the Shafton seam near Barnsley, Yorkshire (Westphalian C), this was the most abundant type of megaspore present. A specimen from this source is shown in Pl. 44, fig. 11. A histogram of size variation in 100 megaspores from this seam compared with the smaller number extracted from *Selaginellites canonbiensis* sp. nov. is shown in text-fig. 2. The isolated *Setosisporites hirsutus* from the Shafton seam show a rather larger proportion of branched to unbranched hairs, and have less sharply defined contact faces than the megaspores of *Selaginellites canonbiensis* sp. nov.; despite this, the megaspores in the cone, if found isolated, would be correctly included in *Setosisporites hirsutus*.

THE MICROSPORES

On maceration the contents of the microsporangia disintegrated almost completely into individual spores (Pl. 44, figs. 4–7, text-fig. 4A and B), leaving some clusters and



TEXT-FIG. 2. Histograms showing the similarity of size distribution in *Setosisporites hirsutus* from the Shafton Coal, Yorkshire, and megaspores extracted from *Selaginellites canonbiensis* sp. nov. The largest dimension of the spore was measured in each specimen. Based on 100 of the isolated spores and 13 from the cone. (Slides nos. Mik (C) 278–81 incl.; Kidston Collection nos. 3154A and B, 3153D, Geological Survey and Museum, London.)

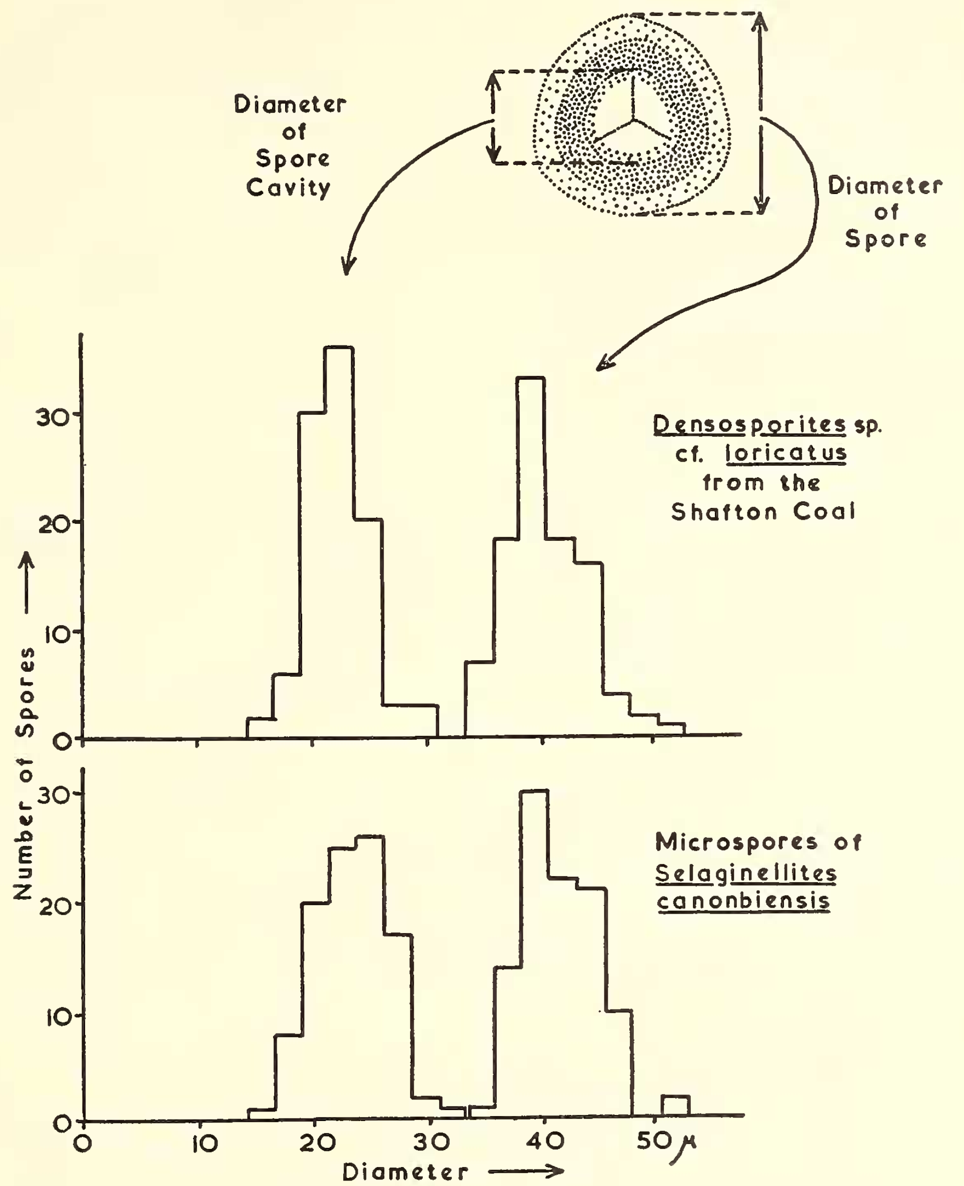
occasionally individual tetrads still adhering together. A number of preparations were made, representing several hundred microspores; all were of essentially the same type, and no obviously different (i.e. foreign, contaminating) spores were seen. A histogram based on two measurements (inner diameter of the spore, and overall diameter) of each of 100 spores is shown in the lower half of text-fig. 3. This is at least consistent with the hypothesis that the spores represent a single population, namely the original contents of the cone. The spores range from 36–53 μ diameter with a mean of 43 μ.

The spores were originally oblate, with a round to subtriangular equatorial outline. The equatorial zone of the spore was apparently greatly thickened so as to form a rim (the *cingulum* of Potonié and Kremp) diminishing in thickness towards the periphery. The proximal and distal faces of the spore were evidently very thin and are often torn or missing. The triradiate marking is sometimes evident as three sutures or slits in the proximal face which extend only as far as the inner edge of the cingulum (text fig. 4).

Spores similar to the microspores of *Selaginellites canonbiensis* sp. nov. are a common constituent of Carboniferous coals, and have been assigned to the spore genus

Densosporites. Of the Upper Carboniferous species cited by Potonié and Kremp (1956*a*) the spores in the cone show best agreement with *D. loricatus* (Loose) S.W. and B.

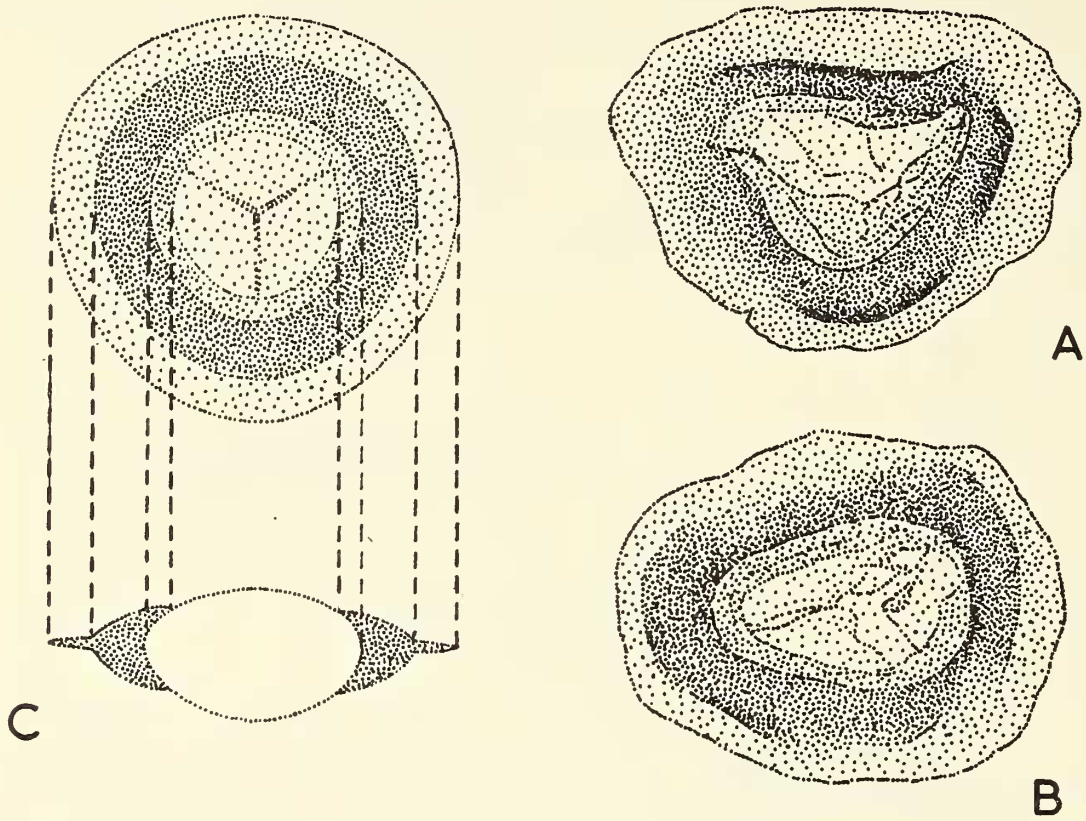
The sample of the Shafton Coal which contained abundant megaspores agreeing with those in *Selaginellites canonbiensis* sp. nov. was also examined for small spores. A species of *Densosporites* similar to *D. loricatus* was found to be more abundant than any other



TEXT-FIG. 3. Histograms showing the similarity of size distribution in populations of *Densosporites sp.* cf. *loricatus* from the Shafton Coal, and microspores from *Selaginellites canonbiensis*. Each population gives two sets of measurements; the inner diameter of the spore cavity, and the overall diameter. Based on 100 spores of each population. (Slide nos. Mik (C) 276; Kidston Collection 3153A and B, Geological Survey and Museum, London.)

single spore type present. One of these spores from the Shafton Coal is shown in Pl. 44, fig. 8 (the optical density of the spore in this photograph is exaggerated by its being stained with safranin). The demarcation between the inner (darker) zone of the cingulum and the outer (lighter) zone is not so marked as in the microspores from the cone, but otherwise they show good agreement. A histogram based on 100 spores from this coal is shown above that of the microspores from *Selaginellites canonbiensis* sp. nov. in text-fig. 3.

It seems reasonable to suppose that these isolated small spores (*Densosporites sp.* cf. *loricatus*) and the larger *Setosisporites hirsutus* occurring together in the Shafton Coal were produced by a single species of parent plant which was closely similar to *Selaginellites canonbiensis* sp. nov. It does not follow that all Upper Carboniferous spores assigned to the genera *Setosisporites* and *Densosporites* represent the megaspores and microspores respectively of *Selaginellites*; but this is probably so for at least some other species of the three genera concerned.



TEXT-FIG. 4. A and B, two microspores from *Selaginellites canonbiensis* sp. nov., $\times 1{,}000$, showing the thicker and thinner parts of the cingulum. C, a diagrammatic reconstruction at the same scale, showing the unflattened spore in plan and polar section (with the proximal face uppermost). (A and B from slide 3153C, Kidston Collection, Geological Survey and Museum, London.)

TAXONOMIC POSITION OF THE CONE

The genus *Selaginellites* was first described by Zeiller (1906). His species (*S. suissei*) was based on a number of specimens which were similar to typical *Selaginella* species in two important respects. Firstly, they were heterosporous, with *Selaginella*-like terminal cones; and secondly, the leafy shoots were heterophyllous (a character of many, but not all, living Selaginellas). Zeiller (1906), Halle (1908), and Seward (1910) have recommended that *Selaginellites* should be reserved for those fossil *Selaginella*-like forms known to be heterosporous. Subsequently two petrified Carboniferous *Selaginella*-like cones have been described: one of these (Darrah 1938) was actually placed in the genus *Selaginella*; the other (Hoskins and Abbott 1956) in *Selaginellites*. Although nothing is known of the vegetative structure in these cases, the attachment of the sporangia and the presence of a ligule are additional features of agreement with *Selaginella*. Finally, Lundblad (1948) has assigned to *Selaginellites* a small heterosporous lycopod cone compression. This constitutes a reasonable extension of the use of *Selaginellites* to include a small detached heterosporous cone lacking direct evidence as to its vegetative parts.

The detached cone described here is in the same category as Lundblad's cone in that no direct evidence as to the nature of its parent plant is available. The cone is associated with some fine leafy shoots but the identification of these with *Lycopodites*, *Selaginellites*, *Bothrodendron*, &c., is questionable (cf. Zeiller 1888, pp. 486–96; Němejc 1947, pp. 72–73; Chaloner 1953, pp. 286–7). The general morphology of the cone is *Selaginella*-like; it is far smaller than typical *Lepidostrobus*, and indeed is smaller than several species of *Selaginellites*. The evidence for the affinity of *S. canonbiensis* sp. nov. is to this extent exactly comparable with that on which Lundblad assigned her Triassic cone to *Selaginellites*. This involves a broad interpretation of the genus, and must be subject to any new evidence as to the vegetative character of the parent plant.

COMPARISON WITH *POROSTROBUS* NATHORST

Nathorst (1894) described a small cone (5·5 mm. diameter) from the Lower Carboniferous of Spitzbergen as *Lepidostrobus zeilleri*. Later (1914), he suggested that it should be placed in a separate genus for which he proposed the name *Porostrobus* on the basis of its association with *Porodendron*, although he acknowledged that the connexion with that genus had not actually been demonstrated. In his later paper, Nathorst (1914, pl. 5, figs. 15 and 16) illustrated microspores obtained from this cone by maceration, and from his figures these spores are evidently similar to *Densosporites*. Examination of a slide prepared by Nathorst in the Kidston Slide Collection (Glasgow University) confirms this. Although the microspores are rather poorly preserved they evidently possessed a greatly thickened cingulum. Nathorst was unable to make a clear preparation of the megaspores, which were about 500 μ in diameter.

All that is known of Nathorst's specimen is that it is a small heterosporous lycopod cone detached from its parent plant. On this basis a case could be made for placing it in *Selaginellites*, rather than its being made the holotype of a distinct genus. Its main significance in this context is in its showing a further correlation of an undoubted species of *Densosporites* with another small lycopod cone similar to *S. canonbiensis*.

COMPARISON WITH A CONE ATTRIBUTED TO *BOTHRODENDRON*

Watson (1908) attributes a small petrified megaspore-bearing cone to *Bothrodendron mundum* on the basis of stelar anatomy and other more indirect evidence. The megaspores in this cone show some similarity with those in *Selaginellites canonbiensis* sp. nov. but the hairs on them are much longer, and are restricted to the equatorial zone, where they form a broad fringe around the spore. In this respect they differ also from the isolated megaspores *Setosisporites hirsutus*. As this is the type species of *Setosisporites*, it seems unwise to base a correlation of this spore genus with *Bothrodendron* (cf. Potonié and Kremp 1956*b*, p. 72) on the evidence of Watson's cone.

The megaspore structure is the only feature on which detailed comparison between *S. canonbiensis* and Watson's cone may be made, owing to their different modes of preservation. For the reasons cited above, this comparison indicates that the cones are at least specifically distinct.

ECOLOGY OF *SELAGINELLITES CANONBIENSIS* SP. NOV.

A number of spore workers have remarked on the frequent association of *Densosporites* with so-called splint-coals (e.g. Schopf *et al.* 1944, p. 40). Kremp (1952) and Smith